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THE ANATOMY OF SIPHONOPHORA ROSARUM, WALK., THE "GREEN-FLY" PEST OF THE ROSE-TREE.

PART I. THE APTEROUS VIVIPAROUS STAGE.

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(Plate I and 15 Text Figures.)

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Introduction.

WHEN beginning this investigation it was my intention to make a comparison between the anatomy of the apterous viviparous form and that of the winged viviparous form, to ascertain what differences were present corresponding with the difference in habit of the Aphis in these two stages. I found, however, that the literature bearing on the group to which *S. rosarum* belongs, was somewhat scanty, and as a rule, rather out of date. It therefore became necessary, before undertaking the

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comparative work, to obtain a somewhat more complete account of the general anatomy. It is with this idea in view that the following paper has been written; but, as will be seen on perusing it, much more attention has been given to the internal anatomy than to the external parts. It is my intention, now that this first part of the task is completed, to take up my original project. I desire to take this opportunity of expressing my gratitude to Professor Bridge, Mr A. E. Shipley, F.R.S., Mr Doncaster and Mr Collinge for the valuable assistance and advice they have given me whilst this work has been in progress.

Methods.

The extremely small size and delicacy of the insects dealt with entailed somewhat careful manipulation. To obtain a good supply of material, rose trees were infested, as far as possible, with *S. rosarum* only. In this way a fresh supply of good material was always ready at hand. For fixing, Petrunkewitsch's modification of Gilson's fluid was used, the formula being :

Water (distilled)	30	parts.
Absolute alcohol	20	parts.
Glacial Acetic Acid	9	parts.
Nitric Acid (pure)	1	part.

Corrosive sublimate to saturation.

For staining the sections, Naples Carmine, Ehrlich's Haematoxylin, and Weigert's Elastic tissue stains were used.

In order to confirm results obtained from the serial sections dissections were made; and for this purpose I found the large binocular dissecting microscope made by Zeiss of the utmost use. The microscope was the one having the alterations suggested by Braus and Drüner, and the large working distance possessed by its lenses gave great facility in work performed under it. The instrument is to be strongly recommended for such minute work as the dissection of Aphides. The dissections were carried out in glycerine.

Whilst engaged on the tracheal system, I found that a very effective way of showing up the details of the system was to kill and mount a few specimens in hot glycerine jelly. The effect was that the jelly in cooling, stopped up the stigmata, preventing the escape of the air, and yet penetrating sufficiently to render the animals transparent. Care must be taken not to overheat the jelly, or the heat will drive the air from the tracheae before the jelly has solidified sufficiently to stop up the stigmata.

Whenever possible, the drawings were made with the camera lucida, and in the diagrammatic ones the proportions were obtained from camera lucida sketches.

External characters.

Buckton (1875—1882), in his Monograph, gives the distinguishing features of *S. rosarum* as follows:

Long, oval, flat. Wholly green, ringed, the posterior edges fringed with capitate hairs which mostly spring from small tubercles. Vertex tufted. Antennae and legs somewhat short. Frontal tubercles small. Eyes reddish brown. Tail green, and not conspicuous.

This description certainly includes most of the distinguishing features of *S. rosarum*; and it is only intended here to give in more detail points not brought out in the above description.

The body consists of head, thorax and abdomen; the first two together forming the anterior half of the body and the abdomen the posterior half (Text Figs. 1 and 2).

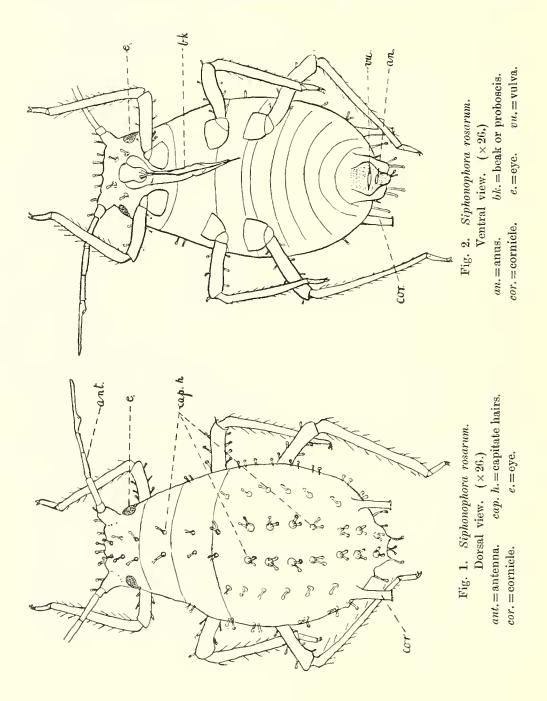
The segmentation of the body is not so markedly clear as Buckton seems to infer. The three segments of the thorax are fairly distinct, and, on the ventral surface only, the segments of the abdomen can be made out, but they are almost invisible on the dorsal surface.

When the Aphis is viewed from above, the most striking feature is the rows of capitate hairs (cap. h.) which Buckton mentions. These are arranged in six rows-three on each side of the median line (Text The two middle rows are more prominent than the others Fig. 1). from the fact that the tubercles or excrescences upon which the hairs are mounted, are more pronounced than in the other cases. Moreover. in these median rows each tubercle bears two hairs and the rows are continued right to the front of the head. In the other cases the rows are confined mainly to the abdomen. These hairs are also found for a short distance on the legs, usually ceasing at the beginning of the tibia, so that towards the end of that joint the hairs are of the usual tapering kind. A remarkable feature about the feet of the Aphis is the reduction of the number of the tarsi to one (Text Fig. 4). This is described by Buckton. The antenna (Text Fig. 5) of S. rosarum-in common with all the genus Siphonophora—consists of six joints. The last joint is very peculiar, it being composed of two parts—an expanded

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portion forming the base and terminating in a more slender part. The whole of the surface of this joint is covered with small ridges giving it quite a remarkable appearance (Text Fig. 6). The significance of these ridges is open to conjecture, but probably they indicate the presence of some kind of sense organ.

The only definite sense organs which S. rosarum has are the eyes,



and these present no differences from those of other Aphides. Behind each eye is a small ocellus, or supplementary eye, possessing usually two facets (Text Fig. 7). Each eye and ocellus is supplied by a large nerve (*n. e.* Plate I, Fig. 20) from the optic lobe of its side. This nerve expands at the base of each eye, and from this expansion, nerve fibrils are given off to the ommatidia of the eye and ocellus.

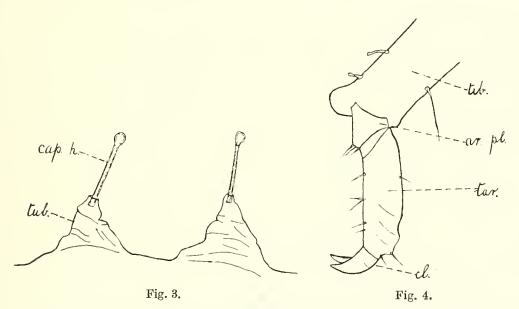


Fig. 3. Two capitate hairs and the tubercles from which they spring seen in profile. $(\times 230.)$ cap. h.=capitate hair. tub.=tubercle.

Fig. 4. Tarsus of third leg. $(\times 355.)$ ar. pl.=articulatory plate of the tarsus. cl.=claw. tar.=tarsus. tib.=tibia.

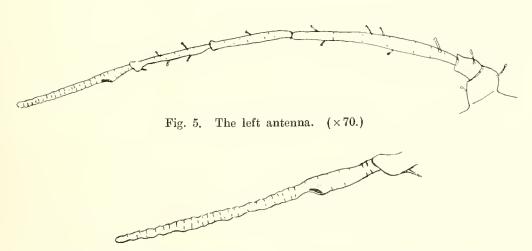


Fig. 6. The last joint of the antenna to show its remarkable appearance. $(\times 152.)$

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The tail or cauda is, as Buckton says, quite inconspicuous, and is scarcely visible from the dorsal surface. It is completely covered with short stumpy hairs, which also surround the anal and reproductive apertures.

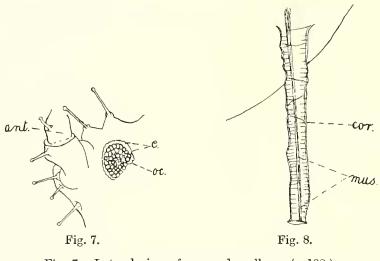


Fig. 7. Lateral view of eye and ocellus. (×108.) ant.=antenna. e.=eye. oc.=ocellus.
Fig. 8. A cornicle or nectary. (×100.) cor.=cornicle. mus.=controlling muscle.

The Alimentary Canal.

The alimentary canal of Aphides in general has been figured from time to time by various authors, among whom may be mentioned Dufour (1833), Buckton (1875—82), Witlaczil (1882), and others.

Witlaczil's figure of the alimentary canal of *Aphis pelargonii* agrees in many points with the results I have obtained.

The alimentary canal presents many remarkable features, the most striking of which is the complete absence of pyloric caeca or malpighian tubules. Dufour, among the earliest investigators of this part of the anatomy, expresses his astonishment thus :—

"L'appareil digestif des Pucerons présente une exception fort remarquable, unique......; c'est l'absence absolue des vaisseaux hepatiques."

The alimentary canal (Text Figs. 9 and 10) commences at the oral aperture which is situated on the lower posterior side of the head, and is so placed that it lies in close connection with the groove which traverses the whole length of the upper surface of the proboscis or beak,

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and which receives the setae after they leave the head. The mouth opens into an extremely narrow oesophagus which extends first in a vertical direction towards the dorsal surface of the head, passing on its way through the loop made by the circum-oesophageal connectives. On

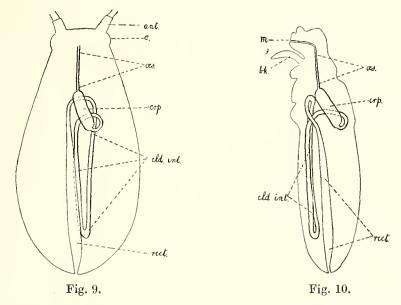


Fig. 9. Dorsal view of alimentary canal. Semi-diagrammatic. (×20.) ant.=antenna. cld. int.=coiled intestine. crp.=crop. e.=eye. rect.=rectum. Fig. 10. A lateral view of the alimentary canal. Semi-diagrammatic. (×20.) bk.= beak or proboscis. cld. int.=coiled intestine. crp.=crop. m.=mouth. oes.=oesophagus. rect.=rectum.

reaching a position about two-thirds of the distance from the ventral to the dorsal surface, the oesophagus turns abruptly backwards and continues in the median line to a position in the anterior portion of the mesothorax. At this point—in an external view—the narrow oesophagus dilates abruptly to form the crop or stomach, but, seen in section, the oesophagus is continued for a short distance into the interior of the crop, thus causing a slight invagination of the anterior end of the latter. In this way an effective valve is formed to prevent the fluid poured into the crop passing back again into the oesophagus. This point was observed and figured by Witlaczil (1882), and is shown in Fig. 13 (Plate I). The crop is the widest portion of the alimentary canal, and generally lies in an oblique position, its posterior end pointing towards the right and dorsal sides of the body. The crop then gives place to the coiled intestine which is considerably narrower than the crop, but has a lumen very much larger than that of the oesophagus. The curves of this part of the alimentary canal vary in different individuals, and in many cases they are complicated by the contraction of the abdominal segments at death. In the Text Figs. 9 and 10 are represented diagrammatically coils which are present in every individual, but complications in the form of smaller supplementary coils may occur. Commencing at the crop, the coiled intestine inclines towards the right, and in doing so, curves completely round, dips down, passes beneath the crop, and reaches a position on the ventral surface, slightly to the left of the median line. From this point, it proceeds in a posterior direction to about the middle of the abdomen; then, curving abruptly, returns forwards until the region of the crop is again reached. Here it makes its final curve, and rising above the last-mentioned coil, takes a direct course to the anus which is placed at the posterior end of the body. In this last coil the intestine merges into the rectum, which at first widens gradually, beginning to narrow again as it approaches the anus. The supplementary coils mentioned above usually occur where the alimentary canal makes its backward curves.

The mouth is bounded by four separate structures each contributing towards the formation of the oral cavity. The anterior margin is bounded by the pointed labrum (see Plate I, Fig. 12), and the posterior margin is formed by a part of the labium which takes the form of a small under-lip, while the remainder of the labium constitutes the beak or proboscis. Laterally, the mouth is bounded by two down-growths from the sides of the head, and these fit in between the labrum and the small under-lip,—the whole enclosing the small oral cavity. The setae in their course out of the head pass through this oral cavity, and the labrum has a marked groove on its inner side in which they are lodged before they leave the head altogether to lie in the groove in the upper surface of the beak.

The mouth organs of S. rosarum agree in some points with those of other—and in some cases more specialised—Aphides, described by Witlaczil (1882), Krassilstschik (1892 and 1893), Drefus (1894), etc. One point of difference, however, is that my investigations fail to reveal any definite organ which is at all comparable to the salivary pump described and figured by them in other genera.

Witlaczil (1882), in his description of the mouth organs of Aphides, leaves several points somewhat obscure, more especially with regard to the number and condition of the setae. The setae of all the Hemiptera have attracted a great deal of attention, because there seems to be some doubt as to their true homology; but it is not intended in this paper to enter into that discussion, but rather to give as accurate an account as possible of the mouth organs of the species under consideration.

S. rosarum, like other Aphides, possesses a chitinous framework in the head for the support and control of the mouth organs. Whether this corresponds to the tentorium usually present in the head of insects is rather doubtful; at least it is much more complex than the usual type of tentorium. Fig. 1 (Plate I) gives a general frontal view of this chitinous framework, and it agrees in some points with the figures given by Witlaczil and Krassilstschik; but, at the same time, there are points of difference, especially in connection with the lower parts.

It will be necessary first to describe in detail this framework, and in doing so, reference will be made to similar arrangements in other Aphides.

The chitinous framework. Traversing the head from side to side, in a position about two-thirds of the distance, dorso-ventrally, from the ventral side of the head, there is a strong, hollow, slightly curved rod of chitin, which is closely applied to the under surface of the cerebral ganglia (see Plate I, Fig. 4). From this rod the whole of the chitinous framework depends, and to it most of the muscles controlling the mouth parts are attached. Compared with the figures of Mark (1877), Krassilstschik (1892 and 1893), etc., this rod corresponds with their "Arcus superior," but I think the term "Transverse bar" is more appropriate. This bar has two pairs of chitinous supports, which may be termed the "Anterior and Posterior lateral rods," one pair arising from its anterior face, and the other pair from its posterior face. These supports arise from the ends of the bar, and consist of slender hollow rods of chitin, joining the bar to various parts of the head. The anterior lateral rods pass almost horizontally forwards, closely applied to the under surface of the expanded portion of the cerebral ganglia, so that the tapering portions of the ganglia lie between them. This pair eventually becomes continuous with the chitin of the front of the head. The posterior lateral rods dip down at a considerable angle and finally become connected with the ridge which marks the junction of the head with the first thoracic segment.

Depending from the centre of the tranverse bar or rod are two rodlike pieces of chitin which are arranged in the form of an inverted V (Λ), the junction of the two arms corresponding with their point of attachment to the transverse bar. The arms of the Λ -shaped bar are divided towards the lower end by a kind of joint, and finally they both make a strong curve inwards and become continuous with the chitin of the floor of the front of the head. The lower part of each arm—that is from the joint downwards—has attached to it two curved rods of chitin, placed one above the other, and projecting one forwards and one backwards into the head. The more dorsally placed rod from each side is continuous with the expanded base of the anterior seta of that side, and the lower rod from each side is attached to the base of the posterior seta. In this way, the transverse bar, the arms of the Λ , and the setae themselves are all in direct continuity with one another. This point will be dealt with again in connection with the protrusion of the setae.

In the description of the pharynx it will be shown that the posterior wall of the pharynx is strengthened by a strong layer of chitin which extends from the mouth aperture to the point where the oesophagus makes its abrupt curve over the transverse bar, and in preparations to show the chitinous framework, this strip of chitin always remains behind and hence it appears in Fig. 1 (Plate I), though it does not actually contribute to the support of the mouth parts. The chitinous skeleton of the front of the head is raised into an ovoid dome, and on the inner surface of the dome the muscles which dilate the pharynx have their origin.

The setue. With regard to these organs, S. rosarum agrees, so far as I am able to judge from the literature at my disposal, with most of the Aphides. The setae are really four in number, but, as Buckton and others have observed, the proboscis or beak only contains three stylets. Witlaczil (1882), figures (Plate II, Fig. 5) Aphis platanoides with four setae in the beak, but I feel sure that this must be an error. Krassilstschik (1893) states that in *Phylloxera vestatrix*, fusion of two setae has taken place, but he does not make it quite clear which pair of setae have fused.

In S. rosarum the setae are arranged in two pairs—an anterior and a posterior pair—and it is the posterior pair which fuse to form a single median seta-like structure. In Fig. 2 (Plate I) will be seen a transverse section across the upper lip or labrum, just where the setae are leaving the head to pass into the groove in the dorsal side of the beak. The three setae are all cut across transversely, and lie in a straight transverse line. On closer examination it will be seen that each of the two external setae has a single clear spot in the centre, which represents a fine tube traversing the whole length of the seta. On looking at the section of the median seta, it will be noticed that there are two clear spots, showing that there are two tubes running down it. This in itself is very good evidence that the median structure

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represents two fused setae. Beyond this, however, the examination of sections transverse to the whole animal, shows that the two posterior setae approach one another and fuse in the middle line, at the same time coming forward, so that the product of their fusion lies between and separates the two anterior setae.

The muscles of the setae. Inserted in the base of each seta is a strong muscle which has its origin at the end of the transverse bar which crosses the head (Plate I, Fig. 4). The muscles, from their position, are obviously retractor muscles, their function being to assist in the withdrawal of the setae from the host plant. These muscles were figured accurately by Witlaczil (1882), but Krassilstschik (1893) states that the retractor muscles in *Phylloxera* are attached to the These authors also figured protractor muscles, front of the head. and Krassilstschik states that they are attached to the chitinous rods which project from the lower part of the arms of the Λ . In S. rosarum I have been unable to find any protractor muscles except a small one attached to each of the posterior setae, but these are quite short and wholly inadequate to perform the function of driving the setae into the host plant, and moreover, these muscles are much smaller than the retractor muscles. Surely it is anomalous to have the greatest force to do the least work, for it is obvious that more force is required to drive the setae into the tissues of the host plant than to withdraw them.

How then are the setae protruded?

The following is a suggestion as to the way in which the operation is performed, but first it will be necessary to give an account of the relations of the muscles in the head to the chitinous framework and the setae.

It will be remembered that in the introduction to the section on mouth parts, it was intimated that *S. rosarum* does not possess a salivary pump such as has been described by Mayer (1874 and 1875), Krassilstschik (1892 and 1893), Drefus (1894), and others. There are structures, however, which are identical in position and general appearance with those described by the above authors, but it seems to me that they serve an entirely different purpose.

In exactly the same position in the small pointed under-lip (probably part of the labium) which closes the mouth on its posterior margin, where the above authors have described the salivary pump, is a small U-shaped rod of *solid* chitin (Plate I, Fig. 7). Moreover, this structure is continuous with the chitin of this part of the head, so

that it is practically immovable. Now stretching between this U-shaped rod of chitin and the transverse bar which crosses the head, there is a very large double muscle. Where this muscle becomes continuous with the transverse bar, it splits up into a number of fine tendon-like slips (Plate I, Fig. 6), just in the same way as the pharyngeal muscles do at their insertion into the anterior pharyngeal wall. From this it may be inferred that the muscle takes its origin from the U-shaped rod of chitin, and that it is inserted into the transverse bar.

This being the case, what will happen when this muscle contracts? One of two things must take place. Either the small under-lip will be drawn up, or the transverse bar will be pulled down. The former is scarcely likely to happen, because the muscle does not lie in the right direction to produce this effect; but more than this, the origin of the muscle is in this under-lip. The only other alternative then is that the transverse bar will be pulled down. The idea that it is the transverse bar which is moved, is supported by the fact that, situated on either side of the middle point of the bar, is a muscle stretching between the bar and the roof of the head (Plate I, Fig. 5), and the only function which these muscles can have, is to restore the bar to its original position after some displacement. It is true that these muscles are small compared with the displacing muscle, but, as will be seen later, they are probably quite strong enough to perform the work they have to do.

Having now described the arrangement and function of the various muscles, we will return to the original problem of how the setae are controlled. First, the strong muscle inserted in the centre of the transverse bar contracts, pulling the bar downwards. The bar in its course will carry down with it the Λ -shaped rods attached to its centre (see Plate I, Fig. 1), and these in their turn will again bring pressure to bear upon the lower jointed parts (j in Plate I, Fig. 1) of the Λ . Now, as has been described before, the rods of chitin attached to this lower part are continuous with the bases of the setae, and my suggestion is that the upper parts pressing on the lower parts of the Λ -shaped rods cause, by the bending inwards of the lower parts, the chitinous rods to take up a lower position in the head, and at the same time carry the bases of the setae along with them; the total effect being, that the setae are protruded more or less vigorously, depending upon the force with which the muscle (l. pr. m.) contracts.

The fact that the posterior pair of setae have a small protractor muscle, does not interfere with the general working of the apparatus, because on looking at Fig. 1 (Plate I) it will be seen that the chitinous rods attached to the bases of these setae are much weaker than those attached to the anterior setae, and it may be that some extra force is required to drive the fused setae into the host plant. From these considerations the name "Large Protractor Muscle" will not be inappropriate for the large muscle which is inserted into the transverse bar.

The next question for consideration is, how are the setae withdrawn? This is probably performed in the following way. First the large protractor muscle will relax. This will cause the chitinous rods, which were probably slightly bent during the process of driving in the setae, to regain their original position by their own elasticity, and then the two muscles attaching the transverse bar to the roof of the head will contract a little and raise the bar a trifle.

The next process is the loosening of the setae in the wound. This will of course be done by the retractor muscles attached to the bases of the setae (Plate I, Fig. 4). It is true that to do this, the retractor muscles will have to bend the chitinous rods attached to the bases of the setae; but it must be borne in mind that the transverse bar, where these muscles take their origin, is stronger than the chitinous rods, so that the muscles can bend the rods without disturbing the transverse bar. Another serious difficulty is whether the setae would be so tightly held in the host plant, that the effect of the contraction of the retractor muscles would be to drag down the transverse bar with the whole chitinous framework attached to it. It must be remembered, however, that the transverse bar is supported in the head by the two pairs of chitinous rods which proceed from either end and are attached to various parts of the head, and also that there are the two muscles stretched between the middle portion of the bar and the roof of the head. Surely these supports will hold the transverse bar rigidly enough for the loosening and partial withdrawal of the setae! Now that the setae are loosened, the only thing that remains to be accomplished is their complete withdrawal, and this will be effected by the two muscles attaching the transverse bar to the head contracting, and thus restoring the whole of the chitinous framework to its original position.

It is highly probable that when piercing the rose-tree, the Aphis does not drive in its setae as one might push an awl into a block of wood, but that the action consists of a continual driving in and subsequent withdrawal or partial withdrawal, for in this way the wound would be continually enlarged, and the movement of the setae in the wound would keep it open and so facilitate the flow of sap.

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From the above account it will be seen that no very close comparison can be made between the mouth organs of *S. rosarum* and those of the other Aphides which have already been figured. The only conclusion one can come to is that there are wide differences between the various groups of Aphides in this respect. Of course one would expect to find some variations, especially in those Aphides which form galls, but it is remarkable that such wide differences should exist in such points as the presence or absence of a protractor muscle to each seta, and also the point of origin of the retractor muscles.

The *pharynx*—the first portion of the oesophagus—is modified, as in all the Hemiptera, to fulfil a suctorial function. It extends from the oral cavity to where the oesophagus turns backwards. The posterior wall of the pharynx is strengthened by a strong layer of chitin, while the anterior wall consists of a flexible but elastic membrane (see Plate I, Fig. 12). Originating from the front wall of the head, and inserted into the anterior wall of the pharynx, where they split up into a number of tendon-like slips, is a double series of muscles. These muscles, contracting, will pull the anterior wall outwards, in that way increasing the capacity of the pharynx, and the oesophageal valve preventing the return of fluid from the crop into the oesophagus, fluid, drawn up the groove in the beak by capillarity, will be sucked up through the mouth into the pharynx.

The muscles then relaxing, the membrane, by virtue of its own elasticity, will return to its former position; and this process commencing at the oral end of the pharynx, the excess of fluid will be gradually forced along the oesophagus into the crop. In this way the insect is able to suck up the sap of the plant which oozes from the wound made by the setae.

The oesophagus presents no remarkable features, structurally, beyond the fact that nuclei and cell boundaries are almost entirely absent—I do not find the series of nucleate cells figured by Witlaczil (1882). The wall is comparatively thick, and composed of fine granular material (Plate I, Fig. 8). The point for remark about the oesophagus, however, is its extremely small size, and, as a natural consequence, the almost ultra-capillarity of the lumen. Dufour (1833) was evidently struck by this fact, for he says in describing this portion of the alimentary canal: "L'œsophage a une ténuité plus que capillaire."

The *crop* consists of a thick-walled, cylindrical sac or bag for the reception of the fluid sucked up from the host-plant by the Aphis. The wall is composed of rather large cells with large nuclei and nuclear bodies, and somewhat granular cell-contents (Plate I, Fig. 9). The

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interior of the crop appears to be always full of fluid which, in the prepared sections, appears as fine granular matter with large clear interspaces. This frequently gives a false impression of a solid crop. This point is illustrated in Fig. 13 (Plate I), which is a camera lucida drawing of a longitudinal section through such a crop.

The coiled intestine is the longest portion of the alimentary canal, and throughout its entire length it is roughly oval in cross-section, being flattened dorso-ventrally (Plate I, Fig. 10). The walls are comparatively thick, and large nuclei with definite nuclear bodies occur at frequent intervals. Cell boundaries, however, are not at all clear, and the nuclei are embedded in a matrix of rather coarse granular matter. This fact, coupled with the large size of the nuclei, suggests a secretory function for this portion of the alimentary canal; and in the complete absence of definite digestive glands, the probability is that this is so.

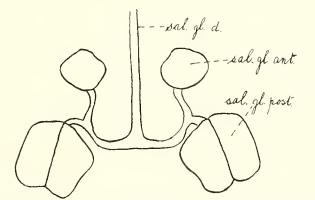


Fig. 11. Dorsal view of the salivary glands. Semi-diagrammatic. $(\times 152.)$ sal. gl. ant.=anterior salivary gland. sal. gl. d.=duct of salivary gland. sal. gl. post.=posterior salivary gland.

The rectum differs greatly from the coiled intestine in structure. For the greater part of its length, it is composed of a network of longitudinal and circular bands of muscle fibres, the circular bands being on the outside (Plate I, Fig. 14). The wall is very much thinner than that of the coiled intestine, and there are only a few scattered nuclei present (Plate I, Figs. 11 and 14). Towards its posterior end, where the rectum narrows, the wall becomes much thicker and is thrown into folds, thus forming a sphincter muscle for the closing of the alimentary canal.

The salivary glands (Text Fig. 11) of S. rosarum are remarkably developed, considering the size of the insect. They consist of two pairs

of unequal size, the anterior pair being smaller than the posterior; and they lie—in close relations with the nervous system—partly in the hinder portion of the head, but mainly in the pro-thorax. Viewed from above, the larger posterior pair lie just in front of, and above, the first pair of thoracic ganglia; while the anterior pair take up a latero-dorsal position,—one on each side of the sub-oesophageal ganglia.

From each gland a duct is given off. The ducts from the anterior glands pass backwards, at the same time dipping down towards the ventral surface. Those from the posterior pair are much shorter, and dip down, passing forwards to meet and fuse with those from the anterior glands. From this point they continue in their ventral course as single ducts, one on each side, closely embracing the nervous system. These two ducts eventually meet and join in the median ventral line, and then proceed in an anterior direction as a single duct, which lies directly beneath the sub-oesophageal ganglion (see Plate I, Figs. 17, 18 and 19). This main duct ultimately opens near the tip of that part of the labium which forms the small under-lip. As has been stated before, S. rosarum has no salivary pump to force the secretion of the salivary glands into the wound made by the setae, and, as it does not form galls, it is probable that the salivary secretion is used to prevent the sap which oozes from the wound in the host-plant coagulating when it comes into contact with the atmosphere. The way in which the salivary secretion is used is probably as follows. The saliva, when the glands are active, will be forced out of the aperture in the small under-lip by the pressure behind of the newly-formed secretion, and perhaps by some contraction of the main salivary duct. It will be remembered that the under-lip is closely applied to the base of the beak or proboscis, and the secretion being poured out from it would naturally run down the groove which traverses the length of the upper surface of the beak. Consequently, it would meet and mix with the sap oozing from the wound made by the setae, and the mixture of the two would then be sucked up into the pharynx and thence into the crop. It is quite possible, therefore, that the salivary secretion, besides preventing the coagulation of the sap, may contain some digestive ferment to assist in digestion.

The salivary glands are composed of very large cells—especially the posterior pair—with closely granular cell contents and large nuclei with well-defined nuclear bodies.

In the posterior pair, the boundaries of the individual cells separate as they pass from the exterior to the interior, leaving spaces between them, and these presumably form channels to conduct the secretion to the duct which leaves the gland (Plate I, Fig. 16). In the anterior pair this is not so marked.

The Nervous System.

The nervous system of the Aphides was for a long while undescribed. Buckton (1875—1882) in his monograph, entirely omits to figure the central nervous.system, as such. Witlaczil (1882) gives figures of the central nervous system of *Aphis pelargonii* and *Pemphigius spirothecae*. These have been very useful for comparison with that of *S. rosarum*. Mordwilko (1895) also gives an account of the nervous system of *Trama* and *Lachnus*.

The central nervous system of S. rosarum, in common with the Aphides in general (as Witlaczil (1882) has shown), is, compared with that of the typical insect, greatly foreshortened, and considerable fusion and elimination of ganglia have taken place; and often it is only the distribution of the nerves which gives a clue to the identity of the ganglia.

The central nervous system (Plate I, Fig. 20) consists of a series of ganglia comprising two cerebral or supra-oesophageal ganglia, each with its optic lobe or ganglion; two sub-oesophageal ganglia; three pairs of thoracic ganglia; and a single median abdominal ganglion. The cerebral ganglia are placed in the head and are joined to the suboesophageal ganglia by the usual circum-oesophageal connectives, which in this case are short and stout. The sub-oesophageal ganglia are connected with the first pair of thoracic ganglia by what seems to represent a remnant of a primitive double nerve-chain.

The three pairs of thoracic ganglia, and the median abdominal ganglion, are massed up together, and lie in a position between the insertions of the first and second pairs of legs.

The ganglia give off nerves which pass to their respective destinations.

The two *cerebral ganglia*, each bearing an optic lobe, occupy nearly the entire cavity of the head. The ganglia themselves are somewhat ovoid, or, better, pyriform in shape, the expanded end being directed towards the dorsal surface of the head, and the more attenuated end towards the ventral side. From the outer lateral surface of each cerebral ganglion arises, partly from the attenuated end, and partly from the lower portion of the expanded end, an optic lobe, which, seen

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from above, appears nearly as large as the cerebral ganglion to which it belongs. Each cerebral ganglion gives off a nerve to the antenna of its side, and a short stout nerve is given off from each optic lobe to the eye and ocellus to which it is adjacent. From the lower and smaller portion of each of these two cerebral ganglia arises a short circumoesophageal connective, joining them up with the sub-oesophageal ganglia, and, through the loop thus formed, the oesophagus passes in its course from the mouth.

From each sub-oesophageal ganglion a nerve is given off which passes forward and is lost among the maze of muscles connected with the mouth parts.

Extending from the sub-œsophageal ganglion is an elongated portion which, as already suggested, probably represents the anterior portion of a primitive double nerve-chain. Joined to this elongated portion is the ovoid mass of nervous material mentioned previously as being made up of three pairs of thoracic ganglia and a single median abdominal ganglion. Each of the paired thoracic ganglia gives off a nerve to its respective leg, and each nerve appears to bifurcate just previous to its entry into the leg. From the abdominal ganglion a

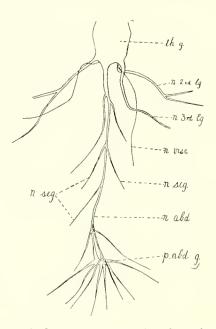


Fig. 12. The distribution of the nerves from the thoracic ganglia, and the median abdominal ganglion. $(\times 54.)$

n. 2nd and 3rd lg. = nerves to the 2nd and 3rd legs.n. abd. = abdominal nerve.n. seg. = nerves to the abdominal segments.n. visc. = nerve to the viscera.p. abd. g. = posterior abdominal ganglion.th. g. = thoracic ganglia.

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stout nerve is given off which extends in the median line to the posterior end of the body. There it expands into a fairly large ganglion from which nerves are given off, which, from their position, must pass to the muscles which control the anal and reproductive apertures. Also nerves are given off from the main trunk during its passage from the median abdominal ganglion to the posterior abdominal ganglion. These nerves are given off fairly regularly in pairs and pass to the segments of the abdomen.

Text Fig. 12 is a camera lucida drawing of a dissection showing this abdominal nerve and the posterior abdominal ganglion with the nerves they give off. In addition to this abdominal nerve, two small nerves are given off from the median abdominal ganglion one on either side of the above-mentioned nerve, and it is to be inferred from their course that they pass to the viscera.

The Tracheal System.

The tracheal system almost completely eluded the efforts of the early investigators like Dufour to figure it with anything approaching completeness.

From the literature I have been able to obtain, it seems that Witlaczil was among the first to give illustrations of the respiratory apparatus of Aphides. He figures the tracheal system of Aphis*pelargonii* (1882), and also indicates the general tracheal system of a Coccid, and the apterous stage of Chermes abietis and Phylloxera quercus (1886). The results I have obtained agree very largely with his representation of Aphis pelargonii. Flögel (1904 and 1905) also describes the tracheal system of the winged female of Aphis ribis, but no figures are given.

Notwithstanding the small size and somewhat sedentary habit of the Aphis in this stage of its life history, the tracheal system is developed to a remarkable degree (Text Figs. 13 and 14).

Situated along the sides of the body are nine pairs of stigmata two pairs being thoracic and the remaining seven abdominal. The first pair is placed in the posterior margin of the first thoracic segment, and the second pair on the anterior margin of the third thoracic segment. The second thoracic segment is entirely destitute of stigmata. The seven pairs of abdominal stigmata are situated—one pair in each—in the first seven segments of the abdomen. The tracheal system is composed of well-defined dorsal and ventral systems—a short trachea

2 - 2

arising from each stigma and dividing into dorsal and ventral branches (Plate I, Figs. 22 and 23).

The dorsal tracheal system. The dorsal branches (Text Fig. 13), when given off from the main trachea, pass along under the laterodorsal surface of the body to a position about two-thirds of the way between the lateral and the dorso-medial lines. In this position, each

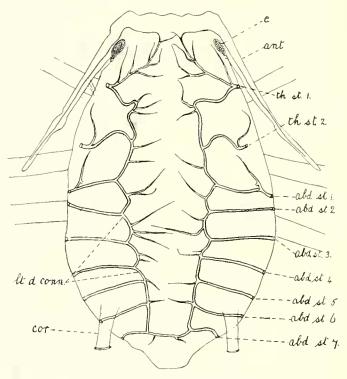


Fig. 13. The Dorsal Tracheal System. $(\times 46.)$ abd. st. 1—7=stigmata of the 1st—7th abdominal segments. ant.=antenna. cor.=cornicle. e.=eye. lt. d. conn.=left dorsal connecting trachea. th. st. 1 and 2=1st and 2nd thoracic stigmata.

branch, with the exception of the first thoracic, divides again into two, and the branches join up to form a single longitudinal trachea (d. conn.)(the Längsstämme of Witlaczil) on each side of the dorso-medial line, extending from the first thoracic segment to the seventh abdominal segment. The course followed by this longitudinal connective trachea is a zigzag one, owing to the subdivisions of the dorsal tracheae meeting at an angle. From each of the long tracheae—one on each side of the median dorsal line—small ramifications are given off into the space enclosed by them. These branches pass downwards and aerate the organs in their immediate vicinity. The right and left divisions of the dorsal system thus formed by the anastomosis of these branches, are not connected with one another except in the seventh abdominal segment, where the posterior branches formed by the bifurcation of the seventh dorsal tracheae meet in the middle line, forming a connection between the two lateral systems.

The first thoracic stigmata. From the first thoracic stigma on each side, in addition to the dorsal trachea which joins the long connective, a large branch is given off near the commencement of the main trachea. This extends in an oblique direction towards the median line of the head, and during its course gives off smaller branches to the surrounding parts. Having arrived at a position opposite to the base of the antenna, it turns abruptly, passes to the insertion of the antenna, and continues along it nearly to its extremity.

The second thoracic stigmata. A lateral branch is given off near the beginning of the dorsal trachea arising from the second thoracic stigma, but this does not give off any supplementary branches.

The abdominal stigmata. Near the commencement of the dorsal trachea which proceeds from the first abdominal stigma on each side, a small branch is given off which extends in an anterior direction. From this the ventral branch in this case originates; in all other cases it is given off from the main trachea proceeding from the stigma. From the sixth dorsal branch on each side, a small trachea is given off to the cornicle, to which it is adjacent. This is not shown in Text Fig. 13, because for some reason it had become invisible in the specimen from which that drawing was taken.

The ventral tracheal system. In this system (Text Fig. 14) it is only the ventral branches given off from the abdominal stigmata which are connected up by the longitudinal trachea. Those from the thoracic stigmata are not so connected. The fusion is effected in exactly the same way as in the case of the dorsal system—the ventral branches, with the exception of the first, dividing when they have reached a position about half way towards the ventral median line, the branches so formed joining up to constitute the long connecting trachea, which, in this case, will only extend from the first to the seventh abdominal segment.

As in the case of the dorsal system, small tracheae are given off from the long connectives into the central space. These dip down and aerate the tissues in their immediate vicinity.

Another feature in which the ventral differs from the dorsal system is that each of the main ventral branches from the opposite thoracic stigmata

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meets and fuses in the middle line with its fellow of the opposite side, so that each pair of thoracic stigmata are connected by a large trachea crossing the thorax transversely. From these tracheae branches are given off to the various parts of the thorax.

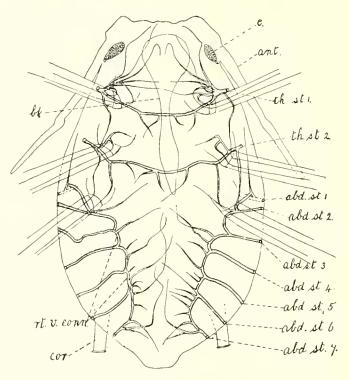


Fig. 14. The Ventral Tracheal System. $(\times 46.)$

abd. st. 1-7 = stigmata of the 1st-7th abdominal segments. bk. = beak or proboscis. cor. = cornicle. e. = eye. rt. v. conn. = right ventral connecting trachea. th. st. 1 and 2 = 1st and 2nd thoracic stigmata.

The *first thoracic stigmata*. From the trachea which connects the first pair of thoracic stigmata, a branch arises on each side near to the stigmata, passes backwards, and enters the second leg of its side. This branch extends to the end of the leg. Two other small branches pass off in the central region towards the hinder border of the first thoracic segment.

A short distance along the main transverse trachea, five branches arise close together on each side, and pass anteriorly. The two outermost ones pass to the front of the head; the next one to the base of the proboscis or beak; and the two innermost ones to the central region of the head. The anterior one of the last-mentioned tracheae approaches its fellow of the opposite side but no distinct fusion takes place between them.

The two tracheae which pass to each of the first pair of legs arise from the last but two and last of these branches—the most anterior one passing to the end of the leg, and the other continuing only to the end of the femur.

The second thoracic stigmata. Near the commencement of the main ventral transverse trachea arising from the second thoracic stigma on each side, a branch is given off which passes directly posteriorly and enters the third leg.

This trachea traverses the leg to its extremity. A little farther along the main trachea, another branch is given off in an anterior direction; from this a sub-branch arises, which turns posteriorly and enters the second leg. In the latter case, however, the trachea only extends to the end of the femur. Still a little farther along the main trachea another branch is given off which passes directly backwards and enters the third leg, but only continues to the end of the femur. The remaining branches from this transverse trachea connecting the second pair of thoracic stigmata, pass to the region traversed by it.

The distribution of the branches to the legs yields reliable evidence —apart from their position—that the two pairs of thoracic stigmata belong to the first and third thoracic segments—each thoracic stigma contributing one branch for the aeration of the second pair of legs to take the place of the tracheae which would arise from the stigmata, were they present, of the second thoracic segment.

The Reproductive System.

The reproduction of the Aphides in this stage of their life history has attracted a great deal of attention from the fact that it exhibits the peculiarity of parthenogenetic reproduction. This being so, there is abundant literature on the subject, but it all—or nearly all—deals with the actual segmentation of the eggs, or with the nuclear changes thus involved.

The morphology of the reproductive system is so simple that the figures given by the earliest investigators still remain almost unaltered to-day.

Dufour (1833), Buckton (1875—1882), Witlaczil (1882) and others give accounts and illustrations of the appearance of this system.

The reproductive system (Text Fig. 15) offers no very remarkable

features from a morphological point of view. It consists of what has been termed a pseudovarium, which is made up of a series of egg tubes arranged in two groups—one on each side of the body.

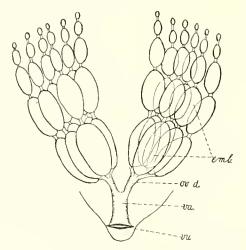


Fig. 15. A dorsal view of the reproductive system. Semi-diagrammatic. $(\times 35.)$ emb.=embryos. ov. d.=oviduct. va.=vagina. vu.=vulva.

The individual tubes of each group meet at their posterior ends, and each opens into a single tube or oviduct. The two oviducts—one from each group—join at the middle line to form a single wide canal—the vagina—which extends to the external aperture—the vulva—situated at the posterior end of the body, just below the anus.

As the Aphis reproduces its kind parthenogenetically and viviparously in this stage of its life history, the egg tubes contain embryos in varying stages of development. As Dufour and others have observed, the embryos always develop with their posterior ends pointing towards the mouth of the tube; consequently they are always born posterior end first.

The two oviducts and the median vagina lie obliquely—dorsoventrally—in the body. As it passes from the vulva, the vagina curves upwards until it lies just beneath the rectum. Here it divides to form the two oviducts, the whole taking the form of a letter Y, in the fork of which the rectum lies. The oviducts continue their upward course the egg tubes lying mainly above the alimentary canal.

The "Secundäre Dotter."

The above is the name given by the German investigators to the masses of granular material found in the body cavity of the Aphis and lying between the egg-tubes. It has also been termed the "Pseudovitellus." I have been unable to determine any definite distribution for it, and the quantity varies in different specimens.

Structurally, it is made up of very large cells (Plate I, Fig. 24) with well-defined nuclei, and the granular cell contents resemble very greatly the yolk of an ordinary insect egg.

Witlaczil (1882) attaches an excretory function to it, but both from its position and structure it is more likely to be nutritive in function.

Circulatory System.

I have been unable to find any structure which would answer to a dorsal vessel or heart in *S. rosarum*, and it is probable that any blood system which may be present consists of a series of haemocoeles.

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REFERENCE LETTERING.

abd. g.	Median abdominal ganglion.
ams. v.	Arms of the inverted V.
an.	Anus.
ant. lat. r.	Anterior lateral rod.
b. se.	Bases of the setae.
bk.	Beak or proboscis.
<i>c</i> . <i>g</i> .	Cerebral ganglion.
ch.	Chitin.
ch. r.	Chitinous rods attached to the lower parts (j) of the arms of the Λ , and joined to the bases of the setae.
cir. oes. conn.	Circum-oesophageal connectives.
circ. mus.	Circular muscle fibres.
crp.	Crop.
<i>d. br.</i>	Dorsal branch of trachea.
d. conn.	Dorsal connecting trachea.
е.	Eye.
el. m.	Muscles stretched between the transverse bar and the roof of the head and
	which serve to lift up the transverse bar after some displacement.
emb.	Embryo.
epi.	Epidermis.
fb.	Fat body.
gr.	Granules.
<i>j</i> .	Jointed lower parts of the arms of the Λ .
l. pr. m.	Large protractor muscle.
lbr.	Labrum.
lm_*	Labium.
long. mus.	Longitudinal muscle fibres.
m. ph.	Muscles for dilating the pharynx.
mus.	Muscles.
n. abd.	Abdominal nerve.
n. ant.	Nerves to the antenna.
n. e.	Nerve to the eye.
n. lg. 1, 2, 3.	Nerve to the 1st, 2nd and 3rd legs.
n. mus.	Nerve to muscles controlling mouth organs.
n. visc.	Nerve to the viscera.
nu.	Nuclei.
nu. b.	Nuclear bodies.
oes.	Oesophagus.
op. l.	Optic lobe.
ov. d.	Oviduet.

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<i>p. m.</i>	Small protractor muscle of the posterior setae.
ph.	Pharynx.
r. m.	Retractor muscles of the setae.
sal. gl. ant.	Anterior salivary glands.
sal. gl. d.	Duct of salivary glands.
sal. gl. post.	Posterior sahvary glands.
se.	Setae.
st.	Stigma.
sub. oes. g.	Snb-oesophageal ganglion.
th. g. 1, 2, 3.	1st, 2nd and 3rd thoracic ganglia.
tr. b.	Transverse bar.
и.	U-shaped piece of chitin which serves as the origin for the large protractor muscle.
va.	Vagina.
v. br.	Ventral branch of trachea.
v. conn.	Ventral connecting trachea.
vu.	Vulva.

EXPLANATION OF PLATE I.

All drawings were made with the camera lucida unless otherwise stated.

- Fig. 1. General frontal view of chitinous framework after preparation with caustic potash to clear away all the mnscles. $(\times 230.)$
- Fig. 2. Transverse section across the tip of the labrum to show the setae cut across. $(\times 1050.)$
- Fig. 3. Longitudinal horizontal section across the lower part of the head to show the chitinous rods joining on to the bases of the setae. $(\times 355.)$
- Fig. 4. Longitudinal vertical section through the head to include one end of the transverse bar. $(\times 108.)$
- Fig. 5. Transverse section through the head to show the course of the large protractor muscle. $(\times 108.)$
- Fig. 6. The insertion of the large protractor muscle into the transverse bar. $(\times 355.)$
- Fig. 7. Origin of the large protractor muscle. $(\times 630.)$
- Fig. 8. Transverse section through the oesophagns. $(\times 630.)$
- Fig. 9. Transverse section through the crop. $(\times 315.)$
- Fig. 10. Transverse section through the coiled intestine. $(\times 315.)$
- Fig. 11. Transverse section through the rectum. $(\times 315.)$
- Fig. 12. Median longitudinal vertical section through the head to show the pharynx and the muscles which dilate it. $(\times 108.)$
- Fig. 13. Longitudinal section through the crop to show the insertion of the oesophagus and the post-mortem appearance of the contents. $(\times 355.)$
- Fig. 14. Longitudinal section through a part of the rectum to show the muscle fibres in the wall. $(\times 355.)$
- Fig. 15. Longitudinal section through an anterior salivary gland. $(\times 630.)$
- Fig. 16. Longitudinal section through a posterior salivary gland. $(\times 630.)$
- Fig. 17. Transverse section through the body in the region of the posterior salivary gland to show the duct from the gland passing round the nervous system to the midventral line. $(\times 152.)$

- Fig. 18. The next serial section to that shown in Fig. 17. In this section the main salivary duct is seen in the mid-ventral line beneath the nervous system. $(\times 152.)$
- Fig. 19. A longitudinal oblique section through the middle region of the body, showing the two salivary glands of one side, the duct from each meeting and joining, and the main salivary duct beneath the nervous system. $(\times 236.)$
- Fig. 20. The central nervous system as seen from above. Semi-diagrammatic. $(\times 152.)$ Fig. 21. Longitudinal horizontal section cutting through an embryo just about to descend
- through the oviduct into the vagina and pass outwards. $(\times 72.)$ Fig. 22. Lateral view of the two stigmata to show the dorsal and ventral divisions of the
- short main trachea from the stigma. $(\times 108.)$
- Fig. 23. A single stigma to show short main trachea. $(\times 630.)$
- Fig. 24. A piece of the "secundare Dotter." $(\times 355.)$

Corrections: In Fig. 1 the chitinous rods (ch. r.) on the left side of the figure should show a cross line as on the right above the upper dotted line leading to ch. r. In Fig. 4 the dotted line leading from p. m. (small protractor muscle) should not traverse the space to the right of the muscle. In Fig. 20 for circ. ves. conn. read circ. oes. conn.; the swelling beneath (opposite n. mus.) represents the sub-oesophageal ganglion.

NOTE.

Since going to press, it has been brought to my notice that the homologies of the Hemipterous mouth parts are now generally accepted. The structures which have been called the anterior setae will therefore represent the mandibles, and the posterior setae, the first maxillae.